



The role of primary visual cortex (V1) in visual awareness

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Abstract

In the search for the neural correlate of visual awareness, much controversy exists about the role of primary visual cortex. Here, the neurophysiological data from V1 recordings in awake monkeys are examined in light of two general classes of models of visual awareness. In the first model type, visual awareness is seen as being mediated either by a particular set of areas or pathways, or alternatively by a specific set of neurons. In these models, the role of V1 seems rather limited, as the mere activity of V1 cells seems insufficient to mediate awareness. In the second model type, awareness is hypothesized to be mediated by a global mechanism, i.e. a specific kind of activity not linked to a particular area or cell type. Two separate versions of global models are discussed, synchronous oscillations and spike rate modulations. It is shown that V1 synchrony does not reflect perception but rather the horizontal connections between neurons, indicating that V1 synchrony cannot be a direct neural correlate of conscious percepts. However, the rate of spike discharges of V1 neurons is strongly modulated by perceptual context, and these modulations correlate very well with aspects of perceptual organization, visual awareness, and attention. If these modulations serve as a neural correlate of visual awareness, then V1 contributes to that neural correlate. Whether V1 plays a role in the neural correlate of visual awareness thus strongly depends on the way visual awareness is hypothesized to be implemented in the brain. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

In the non-dualistic approach to consciousness, visual awareness is mediated by the activity of nerve cells. The question that is specifically addressed in this paper, is to what extent the nerve cells in visual cortical area V1, or primary visual cortex, contribute to visual awareness. In discussing the role of V1 in visual awareness I will use the term visual awareness in the same sense as has been done by Francis Crick and Christof Koch. They have argued for a relatively loose definition of the term as long as so little is known about its nature, neural basis, function, etc. (Crick & Koch, 1998a). Instead of precisely defining the term in psychological terms and then finding its neural substrate, it

will be better to have insights from psychology and neurobiology converge towards a unified concept of visual awareness (Churchland, 1997).

Two important facts set the stage for the present discussion. First, visual awareness cannot be equated to visually guided behaviour as such. This becomes most evident in pathological conditions like blindsight. Here, patients suffering from a lesion to cortical area V1, report to be totally unaware of visual stimuli presented to their blind hemifield, yet are quite capable of guessing correctly about many stimulus attributes. They also seem little impaired in other visuo-motor behaviour such as grasping and eye movements to stimuli in the blind hemifield (Weiskrantz, 1996; Stoerig & Cowey, 1997). Such almost total dissociations between visual awareness and visually guided behaviour have proven difficult to demonstrate in normal observers (Kolb & Braun, 1995). However, it is well known that also in normal observers, stimuli that are not consciously per-

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ceived can modify subsequent behaviour, as has been shown in the many experiments on unconscious priming (Holender, 1986; Merikle, 1992). Moreover, anyone will have had experiences like driving home while conscious thoughts were engaged into something entirely different. Altogether this clearly implies that visual awareness can be dissociated from visually guided behaviour as such; not all visually guided behaviour is conscious.

Second, it is clear that not every stimulus that is picked up by the senses and leads to neural activity, leads to visual awareness. This is already evident from the first point, since unconscious visually guided behaviour will also be mediated by neural structures. In classic text books one might still encounter the statement that cortical neurons provide us with the capability to ‘become aware’ of what the sensory organs tell us. We now know, however, that even when a stimulus evokes *cortical* activity we do not necessarily become aware of it. In blindsight, regions of cortex are activated by stimuli of which the patients are not aware (Sahraie, Weiskrantz, Barbur, Simmons, Williams & Brammer, 1997; Stoerig, Kleinschmidt & Frahm, 1998). But also in normal observers, very interesting findings bearing on this issue were recently reported using a semantic priming paradigm. Subjects were shown masked letter strings of which they were not aware. These were followed by numbers which the subjects had to categorize as larger or smaller than five. A classic priming effect was observed in the sense that the invisible letter strings (e.g. the word ‘three’) increased or decreased reaction times depending on whether they belonged to the same category as the subsequent target number. The striking observation was that neural activity related to the unconscious prime could be traced (by EEG and fMRI methods) up to the motor cortex issuing the commands for the appropriate categorization response (either a left or a right hand lever pull). In other words, the unconscious stimulus evoked cortical neural activity in largely the same way as the conscious stimulus, with mostly quantitative differences (Dehaene, Naccache, Le Clec’h, Koechlin, Mueller, Dehaene-Lambertz, Van de Moortele & Le Bihan, 1998).

These considerations bring us to an important pre-supposition that can be made in the study of the neural correlate of visual awareness: some neural activity is producing visual awareness while other neural activity is not. Apparently, some neural activity is ‘better’ in producing visual awareness than other neural activity and the obvious question thus is what activity falls in the one or in the other category. This question can be approached from two rather different perspectives. The first approach, that we will call the localizationist approach, tries to answer this question in terms of neural structures; which parts of the brain (which subcortical nuclei, which cortical areas) are, and which are not

capable of mediating visual awareness. Or more subtly, what types of neurons, or for example what layers of the cortex, mediate awareness. The second approach, that we will call the global approach, does not try to answer the question in terms of neural structures but rather in terms of specific forms of activity. These specific forms of activity may in principle be mediated by any neuron in any part of the brain. Whether the activity mediates awareness is not determined by what neurons show the activity but rather is an intrinsic property of the activity. Examples may be synchronous oscillations in the gamma range, bursts, or specific modulations of spike rate, as for example also shown in relation to attention. I will evaluate the role of V1 in visual awareness from these two rather different perspectives.

2. The localizationist approach

Before asking whether V1 belongs to the neural correlate of visual awareness (NCVA), one has to consider what can be meant by stating that the NCVA is or is not localized in a particular neural structure. The hallmark of the localizationist approach is the supposition of the existence of what may be called ‘awareness dedicated’ neurons. The activity of such neurons, or groups of neurons, is both necessary *and* sufficient to produce awareness of at least some stimulus attribute. These neurons either reside in special parts of the brain, the awareness dedicated areas, or belong to a particular type, say pyramidal cells in some cortical layer. When these neurons fire we become aware of the visual events encoded by these neurons. Note, however, that this is the most extreme form of the localizationist approach, hardly ever encountered as such. Often it is mitigated in the sense that the activity of awareness dedicated neurons *may* lead to awareness (for example depending on their number, their spike rate, or the co-activation of some other awareness dedicated neurons), while the activity of non-awareness dedicated neurons will never lead to awareness. This is how V1 has been denied a role in visual awareness (Crick & Koch, 1995, 1998a; He, Cavanagh & Intriligator, 1996). It has been argued that the activity of V1 neurons in itself will never lead to visual awareness, or in other words that V1 does not possess any awareness dedicated neurons (see below).

How can we decide whether V1 neurons are or are not dedicated to awareness? We will here address two methods, lesion studies and neurophysiological recordings. The two methods have important caveats but nevertheless have provided us with the most useful data until now. The neuropsychological literature on lesions and their implications for perception and awareness is vast and has often been excellently reviewed (Farah, 1990, 1997). Here, we will only review some data

directly relevant to the issue of whether V1 is necessary and sufficient to mediate awareness. In dealing with neurophysiological evidence on the relation between V1 activity and awareness we will mostly limit ourselves to data obtained in awake behaving monkeys, again focussing on the question whether V1 activity is necessary and sufficient for visual awareness.

2.1. Cortical lesions and the locus of visual awareness

The lesion most relevant to the present discussion is of course one to V1 itself. When V1 is damaged, patients are phenomenally blind; they report ‘not seeing anything’, ‘to have no visual sensation whatsoever’, ‘not being aware of anything happening on that side’, etc. However, when forced to guess about the location, form, size, direction of motion or other attributes of the stimuli that are presented to the blind hemifield, they often perform well above chance, a phenomenon called blindsight (Weiskrantz, 1996; Stoerig & Cowey, 1997). Also in the monkey a behavioural correlate of blindsight is found; the animals report to ‘see’ no stimulus, yet are able to localize them in a forced choice setting (Cowey & Stoerig, 1995; Moore, Rodman, Repp & Gross, 1995). Moreover, monkeys with bilateral lesions to V1 are able to navigate in their environment, pick up food, and so on (Stoerig & Cowey, 1997). Apparently, in the absence of V1, vision can still guide behaviour, while bypassing visual awareness completely. Surprisingly, V1 seems necessary for awareness, but not for all visually guided behaviour (not to imply that in blindsight only awareness is missing and all other visual behaviour is normal, see Farah, 1997).

Two questions remain; first, does V1 only *seem* necessary, i.e. is the loss of awareness in fact caused by the V1 lesion depriving other parts of the brain, the ‘real’ awareness dedicated areas, from their visual inputs; second, is V1 also sufficient for visual awareness? V1 provides the input to the extrastriate areas and from there information is transferred either to the parietal cortex (the dorsal stream) or to the temporal cortex (the ventral stream). When V1 is lesioned in the monkey, no visual evoked activity can be recorded any more from the areas of the ventral pathway, in particular V2, V4, and IT (Roche-Miranda, Bender, Gross & Mishkin, 1975; Payne, Lomber, Villa & Bullier, 1996; Nowak & Bullier, 1997). Neurons in area MT, which is part of the dorsal stream, however, remain responsive, with tuning characteristics that hardly differ (Rodman, Gross & Albright, 1989). These responses are probably mediated by the superior colliculus (SC), since a combined V1 and SC lesion fully abolishes the responses (Rodman, Gross & Albright, 1990). Also in humans there is evidence that areas in the parietal lobe are active in blindsight patients, but whether this occurs also when stimuli are not consciously perceived is more controver-

sial (Barbur, Watson, Frackowiak & Zeki, 1993; Stoerig et al., 1998). An alternative explanation for the V1 lesion resulting in a loss of awareness therefore could be that the awareness dedicated areas reside somewhere in the ventral pathway. Indeed some have argued specifically for the hypothesis that the ventral stream mediates perception, while the dorsal pathway mediates visually guided behaviour in the absence of awareness. The hypothesis is further corroborated by the finding that strong dissociations exist between action and perception (Milner, 1995; Milner & Goodale, 1995; see also Goodale, this volume). To find out, however, whether ventral stream activity without V1 can mediate awareness, one would have to be able to activate areas in the ventral stream in the absence of V1, for example by microstimulation. To date, such experiments have not been performed.

How about whether V1 is sufficient to produce visual awareness? Several experiments suggest that this is not the case. First, lesions to the right parietal lobe may cause neglect or extinction syndromes (Vallar & Perani, 1986; LaBerge, 1997). This is a complicated family of disorders (that we will certainly not discuss in detail here), but a common feature is that either the part of the hemifield, or the parts of objects that are contralateral to the lesion are not attended to at all (neglect), or are ignored when ipsilateral stimuli are present (extinction). The precise relation between attention and awareness is still unknown, but at least the two seem intimately related (Merikle & Joordens, 1997). In fact, neglect patients behave as if not aware of the contralateral stimuli (Farah, 1997). Remarkable correspondences furthermore exist with the blindsight phenomenon: also in neglect patients, forced choice or priming procedures can elicit responses to stimuli that are consciously ignored (Farah, 1997). Similarly, neglected stimuli may be able to bias responses to, or modify percepts of attended stimuli (Driver, Baylis & Rafal, 1992; Mattingley, Davis & Driver, 1997). Of course the parietal lesion in itself does not interrupt the flow of information from the retina to V1 (and from thereon to the ventral areas). Apparently, V1 (or ventral stream) activity in itself is not sufficient for the stimuli to normally enter awareness in these patients. Second, Nakamura and Mishkin (1980) reported that a lesion to all non-visual cortex in monkeys renders them ‘behaviourally blind’. The animals were unable to report about visual stimuli, and it was argued that visual information from the lesioned hemisphere could, in principle, have been reported by the animals using the intact connections from visual cortex to the contralateral hemisphere, where motor areas were intact. Evoked potentials could still be recorded from V1 in these animals, showing that the visual cortex was active. The finding is somewhat related to the report of a lesion to the extrastriate areas such that V1 seemed isolated from the rest of the brain

(Bodis-Wollner, Atkin, Raab & Wolkstein, 1977). Here also, evoked potentials from V1 could be recorded, yet the patient was blind.

All in all these findings, although some of them are difficult to interpret, suggest that visual information reaching V1 is in itself not sufficient to mediate visual awareness. V1 is thus not an awareness dedicated area in the strict sense. Note that in drawing this conclusion the ventral stream areas are pulled right away with V1 into the same category of non-awareness dedicated areas, as both in neglect patients and in the non-visual cortex lesions, the ventral areas are still receiving information from V1. As it was already concluded that the dorsal stream areas cannot mediate visual awareness in isolation (see above), it thus finally appears, on the basis of neuropsychological data, that none of the visual areas, V1, extrastriate, dorsal or ventral stream, are both necessary *and* sufficient for visual awareness.

2.2. Neurophysiology and the locus of visual awareness

An second important way of investigating the NCVA is to estimate to what extent neural activity is correlated with perception. Unmistakenly, in V1, activity can be recorded in response to stimuli or stimulus aspects of which we are not aware. Examples exist both in the temporal as in the spatial frequency domain. High frequency (50 Hz) flickering luminance stimuli evoke responses from V1 in experimental animals (Wollman & Palmer, 1995) as well as in humans (Maier, Dagnelie, Spekrijse & Van Dijk, 1987). However, these stimuli are perceived as being of constant brightness, due to the fact that the perceptual flicker fusion frequency is well below 50 Hz. A somewhat related finding is made in relation to colour perception. When two isoluminant colors alternate at frequencies above 10 Hz, one non-flickering (fused) color is perceived that is a mixture of the two component hues. However, cells in the color blobs of V1 respond to the component flicker well above 10 Hz (Gur & Snodderly, 1997). Neurons in V1 furthermore respond to grating patterns of very fine spatial scale (Foster, Gaska, Nagler & Pollen, 1985). This might even occur for gratings that are perceived as homogenous grey surfaces, as humans adapt to the orientation of those gratings even when this orientation is not perceived (He, Smallman & MacLeod, 1995; He et al., 1996). Thus in all these cases there is an aspect of the stimulus that is detected by the V1 neurons, yet that is not perceived.

When random dot patterns are presented in stereoscopic viewing, the pairing of dots presented to the two eyes results in a depth percept. For example, random dot pairs that are presented at a disparity that is different from surrounding dot pairs will readily pop-out from the surround. It has been shown that V1 neurons are tuned to disparity, and this begs the ques-

tion whether this tuning to disparity is related to depth perception or not. This was investigated using anti-correlated dot pairs. Here the dot pairs presented to the two eyes have opposite colors (black versus white). As a result, depth perception is lost. However, V1 neurons seem to be equally well tuned for the disparity of anticorrelated as for the disparity of normal stereo random dot stimuli (Cumming & Parker, 1997). The V1 tuning to disparity thus bears no direct relation to depth perception.

When two differently oriented gratings are presented to the two eyes, the phenomenon of rivalry is observed; subjects perceive either the one or the other grating, and this percept typically changes every few seconds, while the stimulus remains unchanged. Two persons looking at the same rivalry stimulus at the same moment in time might perceive different gratings, and in that sense, the rivalry phenomenon offers a window on 'subjective' aspects of how a stimulus is perceived. Recordings were made in the visual cortex of monkeys that were asked to report their percepts by behavioural means. Many neurons in all areas recorded from (MT, V4, V2, V1) respond to the grating whether it is perceived or not. The response of a percentage of cells, however, is influenced by which of the two stimuli is perceived. This percentage is higher (ca 40%) in higher areas (MT and V4) than in lower areas (V1/V2: ca 20%) (Logothetis & Schall, 1989; Leopold & Logothetis, 1996). Cells in infero-temporal cortex respond in an almost all or nothing fashion to stimuli that are perceived or suppressed in a flash-suppression rivalry paradigm (Sheinberg & Logothetis, 1997).

In summary, many cells in V1 respond to stimulus attributes of which we are not aware, or in other words, many V1 cells are non-awareness dedicated neurons; their activity does not suffice for the percept of the 'invisible' stimulus attributes they encode. Of course that does not exclude the possibility that other V1 neurons do show activity that is correlated to perception and whose activity might be sufficient for that percept. The rivalry experiments show that at least the activity of a small proportion of the cells correlates with what stimulus is perceived. Also, much of the activity of V1 neurons under normal stimulus conditions is obviously in response to stimulus attributes that we do perceive. The question that still remains to be solved is whether this activity is sufficient for visual awareness. Until proven otherwise, the most straightforward conclusion is that V1 does not possess *any* awareness dedicated neurons.

3. A global approach to visual awareness; two candidate substrates

In opposition to the localizationist approach to the

NCVA one finds the global approach. The hallmark of this approach is that the NCVA is not linked to a particular neural structure, but rather to a specific kind of neural activity. In principle this NCVA related neural activity can be mediated by any neural structure, depending on the actual content of awareness. Also the global approaches are hardly ever advocated in the most extreme form; usually the neural structures mediating the NCVA related activity are somehow restricted, for example to the cerebral cortex. I will here investigate the role of V1 activity with respect to two kinds of candidate global NCVA's, synchronous oscillations and amplitude modulations.

3.1. Neuronal synchrony

Synchronous oscillatory neural activity in the gamma range (ca 30–80 Hz) has been proposed as a neural correlate of conscious perceptual organization (Von der Malsburg & Schneider, 1986; Singer & Gray, 1995), or even consciousness in general (Crick, 1994). Synchrony would be a typical example of a global NCVA; at some time neurons may synchronize their activity, while at some other time may be desynchronized, depending on what neurons form dynamic assemblies to represent particular perceptual or motor output events. The representation of a specific conscious event would be at the level of the neuronal assembly (neurons linked by synchrony), not so much at the level of the individual neurons themselves (Edelman, 1992). In the realm of visual perception, individual neurons would only represent individual features of a visual scene, while the synchrony would represent which features group together to form objects.

In support of the hypothesis is that gamma type activity is suppressed under anaesthesia (Kulli & Koch, 1991), and increases under conditions of perceptual or attentional load (Tallon-Baudry & Bertrand, 1999). However, coherent gamma oscillations have been found in the anaesthetized animal as well (Eckhorn, Bauer, Jordan, Brosch, Kruse, Munk & Reitboeck, 1988; Gray, Engel, König & Singer, 1989; Engel, König & Singer, 1991; Singer & Gray, 1995). Synchrony in the gamma range also increases when the reticular formation is stimulated (Munk, Roelfsema, König, Engel & Singer, 1996). Gamma activity may thus represent a general state of arousal, not directly linked to consciousness. Moreover, it is important to distinguish between gamma range oscillations and synchrony per se. High frequency oscillations may primarily serve to facilitate the occurrence of synchrony, particularly over larger distances (König, Engel & Singer, 1995). Synchrony may reflect neuronal group formation also in the absence of oscillatory activity, and it has been proposed that coherent

activity at very different time scales may in fact support the same goal (Roelfsema & Singer, 1998).

What has been studied mostly is the relation between synchrony and grouping criteria of perceptual organization (Eckhorn et al., 1988; Gray et al., 1989; Engel et al., 1991; Freiwald, Kreiter & Singer, 1995; Kreiter & Singer, 1996; Livingstone, 1996; Brosch, Bauer & Eckhorn, 1997). For example, it was found that line segments of the same orientation cause cells in V1 to synchronize their activity more than line segments of dissimilar orientation (Ts'o, Gilbert & Wiesel, 1986; Engel et al., 1991; Livingstone, 1996). At the same time it is known that similarity is a strong grouping factor in perceptual organization. In this way, it has been established that synchrony correlates with the grouping criteria of connectedness, proximity, similarity (common orientation, common direction of motion), and collinearity (Singer & Gray, 1995). What has been less well studied is the relation between synchrony and whether the percepts were processed consciously, or inside the focus of attention, or for example preattentively etc. In fact, many of the experiments were performed on anaesthetized animals, yet a correlate between synchrony and the grouping criteria was still found. An important exception is the study of Fries, Roelfsema, Engel, König and Singer (1997); here it was found that synchrony in the awake cat depended strongly on the dominating percept in a binocular rivalry paradigm.

An important issue is whether synchrony indeed represents the grouping of features in perceptual organization, or rather reflects the direct anatomical connections between neurons that lay the foundations for such groupings. This is a subtle but important difference that we will explain somewhat further. In Fig. 1, putative receptive fields of two low level, say V1, neurons are shown, that are stimulated with bars. In the leftmost constellation (a) the two bars belong to the same object, while in the middle constellation; (b) the two bars belong to two different objects that segregate from each other. If synchrony between these neurons would represent perceptual grouping, a cross-correlation of the spike discharges of the two neurons would have to show strong differences; a higher peak in the correlogram for the homogenous texture stimulus than for the segregating stimulus (see hypothetical correlograms next to label 'perception'). However, we also know that in V1, cells are connected via horizontal fibers that preferentially exist between cells with similar orientation tuning (Ts'o et al., 1986; Gilbert & Wiesel 1989; Malach, Amir, Harel & Grinvald, 1993). On the basis of this alone, we also expect a similar difference in synchrony (see correlograms next to label 'horizontal connections'). The comparison between (a) and (b) therefore does not discriminate between whether synchrony reflects perceptual organization or intrinsic V1

connections. A comparison between stimuli (b) and (c) however will discriminate between the two alternatives. Here different outcomes in synchrony are expected depending on whether synchrony represents perceptual organization or anatomical connections. From the point of view of horizontal connections, low synchrony is expected for both stimuli, since there is a considerable orientation difference between the two stimuli. But as the two line segments belong to a perceptual group in (c), higher synchrony is expected in (c) than in (b) from the perceptual point of view.

This exact experiment has never been performed, but we did something similar. Synchrony between V1 neurons was studied while monkeys were viewing oriented texture displays like the ones shown in Fig. 2(a). The animals reported segregation (i.e. identified the figure from background) both for the 90° and the 20° orientation difference (and of course not for the 0° difference); figures were detected in 89, 89, and 0% of the presentations, respectively. However, synchrony recorded between neurons on either side of the boundary between figure and background reflected the orientation difference rather than the percept, i.e. was high for the 0° and 20° orientation difference and lower for the 90° difference (Fig. 2b). Also for textures segregating on the basis of motion differences no difference in synchrony

was found between segregating or non-segregating stimuli (Lamme & Spekreijse, 1998a). These results clearly demonstrate that the synchrony between neurons in V1 reflect the horizontal connections between cells, irrespective of the outcome of the segregation process.

Also in the early studies using cross-correlation analysis of neuronal activity, synchrony was mainly regarded as reflecting the anatomical connections between recording sites (Ts'o et al., 1986; Gilbert & Wiesel, 1989; Krüger & Aiple, 1989). Experiments on the stimulus specificity of neuronal synchrony suggested that in addition to representing anatomical connections, synchrony was reflecting dynamical associations between neurons that represented features that were perceptually combined into coherent objects (Gray et al., 1989; Engel et al., 1991; Freiwald et al., 1995; Kreiter & Singer, 1996; Livingstone, 1996; Brosch et al., 1997). Most well known is the 'long bar' experiment. In this experiment, it was found that synchronous oscillations between two recording sites were stronger when a single bar co-stimulated the two sites than when two separately moving bars stimulated the sites. The synchrony was weakest when the two separate bars moved in opposite directions (Gray et al., 1989). Closely related is the experiment of Brosch et al. (1997), using moving gratings instead of bars. But also in these experiments

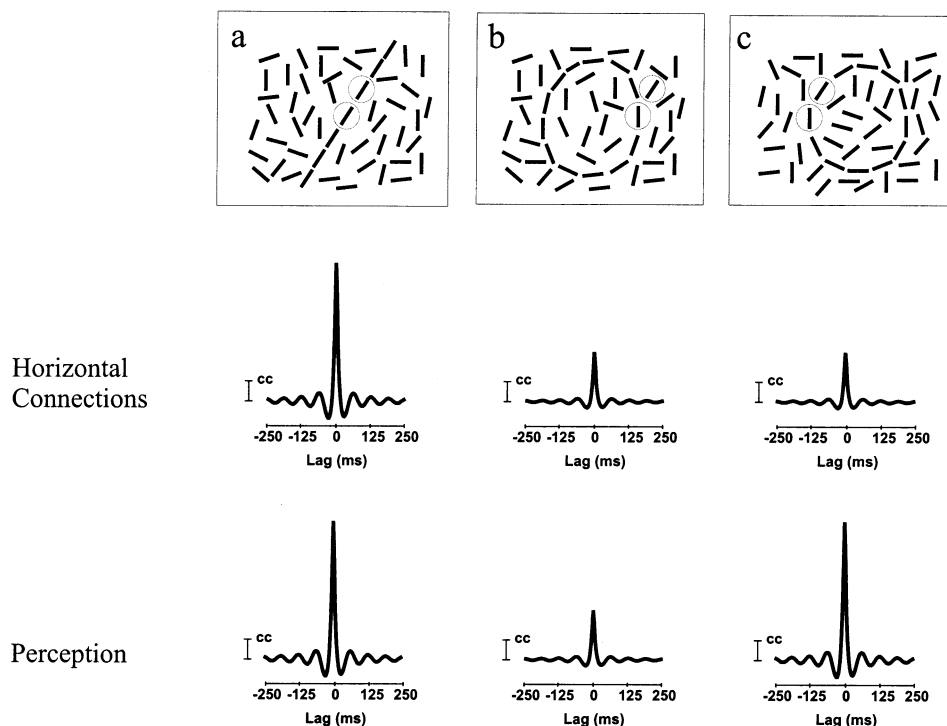


Fig. 1. Three stimuli that can dissociate effects on synchrony. Line segments stimulate two receptive fields (RF's, dotted circles). In stimulus (a) the RF's are stimulated with identical orientations, while in stimuli (b) and (c) the RF's are stimulated with different orientations. When synchrony reflects horizontal connections, that connect cells with similar orientation tuning, cross-correlograms are low for (b) and (c), and high for (a). However, when synchrony transcends the local information, and reflects the perceptual interpretation of the scene, synchrony should be high for both (a) and (c), where the line segment group into a homogenous texture, and low for (b), where the line segments belong to different parts of the scene. cc = cross correlation.

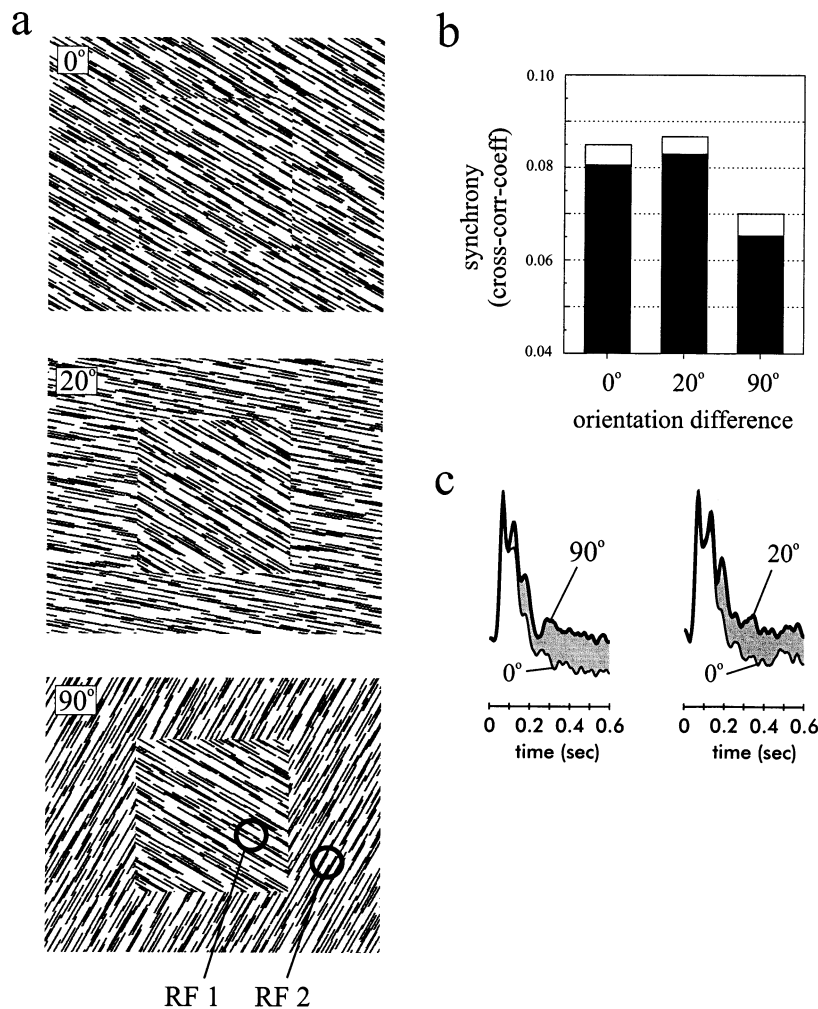


Fig. 2. Synchrony does not, while amplitude modulations do reflect figure-ground segregation in a cue-invariant way. (a) Three orientation differences between a central square and its surround, where both the 20 and the 90° orientation difference result in figure-ground segregation. (b) Synchrony between neurons (whose RF's are shown in (a)), is only lower for the 90° orientation difference, and equally high for the 20° as for the 0° (no segregation) condition. Synchrony thus reflects orientation differences rather than segregation. White parts of histograms give the SEM values. (c) Response amplitudes for the cells with RF1. Both the 20 and the 90° orientation difference give an enhanced response compared with the 0° difference (difference shown as gray shading), signalling the figure-ground segregation rather than the orientation difference.

there is a confound between local (horizontal) connections as such and perceptual grouping. The results can equally well be explained on the basis of connections that depend on distance and orientation selectivity as on the basis of Gestalt laws of grouping: when a long continuous bar is moved, activity of sites representing the bar can spread through local connections from the one end to the other. When two bars move, separated by some gap, the spreading is obstructed by having to transcend a corresponding piece of cortex that is not active. A reduction of synchrony is observed (Gray et al., 1989). When the two bars move in opposite directions, the distance between the two bars is on average even larger, and synchrony reduces further. This interpretation is corroborated by the grating experiment of Brosch et al. (1997). Here, synchrony is reduced when a gap is introduced between two grating fields moving in

the same direction, but not further reduced when the two gratings are also moving in opposite directions (which in this case, contrary to the moving bar, does not on average increase the area of intervening not active cortex). Sadly, the complementary experiment of having the two gratings move in opposite directions without a gap was not performed.

There is also other evidence showing that synchrony depends largely on the architecture of direct cortico-cortical connections (Ts'o et al., 1986; Roelfsema, Engel, König & Singer, 1997). For example, in strabismic cats there is a reduced synchronization between neurons dominated by different eyes (König, Engel, Löwel & Singer, 1993; Roelfsema, König, Engel, Sireteanu & Singer, 1994), which is accompanied by a reduction of connections between different ocular dominance columns (Löwel & Singer, 1992). That synchrony

reflects the dominant percept in binocular rivalry (Fries et al., 1997), cannot easily be explained on the basis of intrinsic V1 connections.

With that one exception, the most parsimonious interpretation of almost all the data seems to be that synchrony in V1 reflects the anatomical connections *within* V1. Neurons are connected on the basis of distance, orientation tuning and collinearity. Only these factors influence synchrony, irrespective of whether the grouping criteria of proximity, similarity and good continuation contribute to the perceptual organization of the scene. One could argue that these connections, and thus the synchrony, lay the initial foundations for the process of perceptual organization, on which higher areas then could further elaborate. This implies, however, that synchrony in V1 does not represent the final outcome of the process of perceptual organization; in other words, the ‘results’ of these further elaborations are not fed back to V1 to update the V1 synchrony. In conclusion, there is very little support for the hypothesis that V1 synchrony is part of the NCVA.

3.2. Modulations of firing rate

A second type of global NCVA would be that visual awareness is expressed in the rate of firing of action potentials of neurons. This would be a correlate of awareness that has many similarities with the correlate of visual attention. It has been shown that in many areas of the visual cortex, including V1, the rate of firing is influenced by whether stimuli are attended to or not (Desimone & Duncan, 1995). This is now generally accepted as the neural correlate of attention. Attention and awareness are intimately interrelated, suggesting that the neural correlates of both may overlap substantially (Posner, 1994; Block, 1996). But aside from that, the correlate of awareness as such might equally well be a modulation of firing rate. In other words, whether stimuli reach awareness or not modulates the rate of firing of cells responding to those stimuli. To what extent is there evidence that V1 activity is indeed a mixture of activity that reflects non-awareness related processing and activity that have a relation to perception?

In contextual modulation, the responses of a cell to a stimulus in its receptive field are influenced by surrounding stimuli. These surrounding stimuli are by themselves not capable of stimulating the cell, but may modulate its firing rate when a receptive field (RF) stimulus is present. The surrounding stimuli may either inhibit or enhance responses to the RF stimulus, depending on the relative characteristics of both RF and surround stimulus. This has been reviewed elsewhere (Allman, Miezin & McGuiness, 1985; Lamme & Spekreijse, 2000). For the present discussion two aspects of contextual modulation are important; its close relation to perceptual organization and its timing.

It appears that contextual modulation is not merely a type of ‘surround inhibition’ but expresses the perceptual interpretation of the elements that make up a scene. Contextual modulation in V1 expresses perceptual pop-out (Knierim & Van Essen, 1992; Kastner, Nothdurft & Pigarev, 1997; Nothdurft, Gallant & Van Essen, 1999). Moreover, more global factors that determine perceptual grouping and segregation of line segments, like for example shown in Fig. 1, likewise influence contextual modulation effects in V1 (Kapadia, Ito, Gilbert & Westheimer, 1995; Polat, Mizobe, Pettet, Kasamatsu & Norcia, 1998). Figure–ground segregation, i.e. whether line segments are interpreted as belonging to the figure surface or the background surface, is expressed under a variety of circumstances (Lamme, 1995; Zipser, Lamme & Schiller, 1996; Lee, Mumford, Romero & Lamme, 1998). Figures can segregate from background on the basis of differences in orientation (Fig. 2), motion, disparity, colour, or luminance, and contextual modulation expresses figure–ground segregation for all these cues (Lamme, 1995; Zipser et al., 1996). Fig. 2(c) shows how contextual modulation signals the figure–ground relationships irrespective of the orientation difference; both the 90 and the 20° orientation difference evoke a similar amount of modulation (where synchrony only ‘signals’ segregation for the 90° orientation difference). Changing the luminance or colour of the background of a coloured square induces a change in the perceived brightness or colour of that (unchanged) square. This is also reflected in the modulation of V1 responses (Rossi, Rittenhouse & Paradiso, 1996; MacEvoy & Paradiso, 1999; Wachtler, Sejnowski & Albright, 1999). In summary, thus, it appears that contextual modulation in V1 expresses the perceptual interpretation of elements in a scene for a wide variety of conditions.

Contextual modulation takes a wide range of times to express itself. Once the cells start to respond, the effects can either occur immediately or only after some latency. The latency of the effects seems to depend on the complexity of the computations underlying the modulation and the spatial extent of the part of the scene that is taken into consideration: the suppressive effect that arises from presenting a stimulus in the immediate surround of a receptive field stimulus takes very short to develop. No latency difference (Müller, Krauskopf & Lennie, 1997), or a latency difference of only 7 ms have been reported (Knierim & Van Essen, 1992). Orientation specific effects, i.e. comparing the effect of an identical background with that of a orthogonal background producing perceptual pop-out, take about 20 ms (Knierim & Van Essen, 1992).

Lamme, Rodriguez and Spekreijse (1999) studied how various aspects of a textured figure–ground stimulus are expressed in the responses of V1 cells at different times. This is shown in Fig. 3. At 30 ms after

stimulus onset the response starts. By comparing responses to textures of different orientations, it can be shown that after 50 ms, orientation tuning (for textures) is expressed by the cells. At around 80 ms, response components emerge that are specifically generated by the figure–ground boundary, consisting of abutting terminated line segments of orthogonal orientation. At 100 ms, an enhancement of the response is found that signals the figure–ground relationship of the surface features that cover the RF. At even later moments in time, neuronal responses in V1 express whether a stimulus is attended to or not: Landman, Lamme and Spekreijse (2000) showed that when multiple figures segregating from background are shown, the initial

phase of the figure–ground modulation did not depend on the number of objects, while at later moments in time (> 200 ms) a relation was found between the strength of modulation and the number of objects in the scene. This suggests that the initial part of the modulation is purely preattentive while at later stages attentive components might emerge. This is line with earlier experiments showing attentional modulation at 235 ms (Fig. 3b, Roelfsema, Lamme & Spekreijse, 1998).

V1 neurons thus express different aspects of visual processing at different times, ranging from simple receptive field based processing up to aspects of fully evolved perceptual organization (see also Roelfsema et

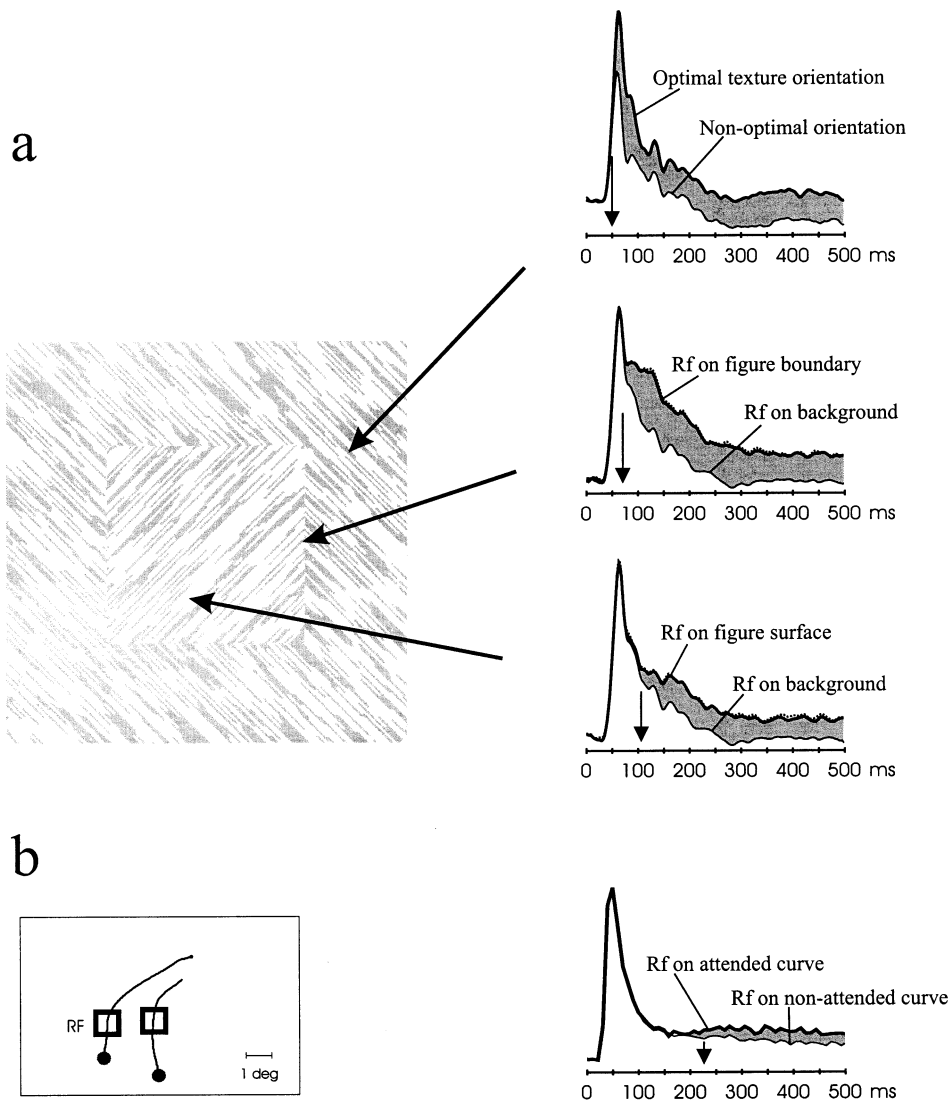


Fig. 3. V1 cells are sequentially selective for various aspects of a stimulus. (a) Comparing responses of V1 cells to differently oriented textures (right column, top graph, gray shading indicates difference) shows that cells are selective for orientation of textures at 55 ms (arrow indicates moment of first significant difference). The same cells are selective for the boundary between figure and ground (second graph from top) at 80 ms, and show an enhanced response when the RF covers the figure surface compared with the background surface at 100 ms (Lamme et al., 1999). (b) V1 cells show an enhanced response when they respond to an attended curve passing through the receptive field (RF), compared with a non-attended curve. This difference occurs at 235 ms after stimulus onset (Roelfsema et al., 1998).

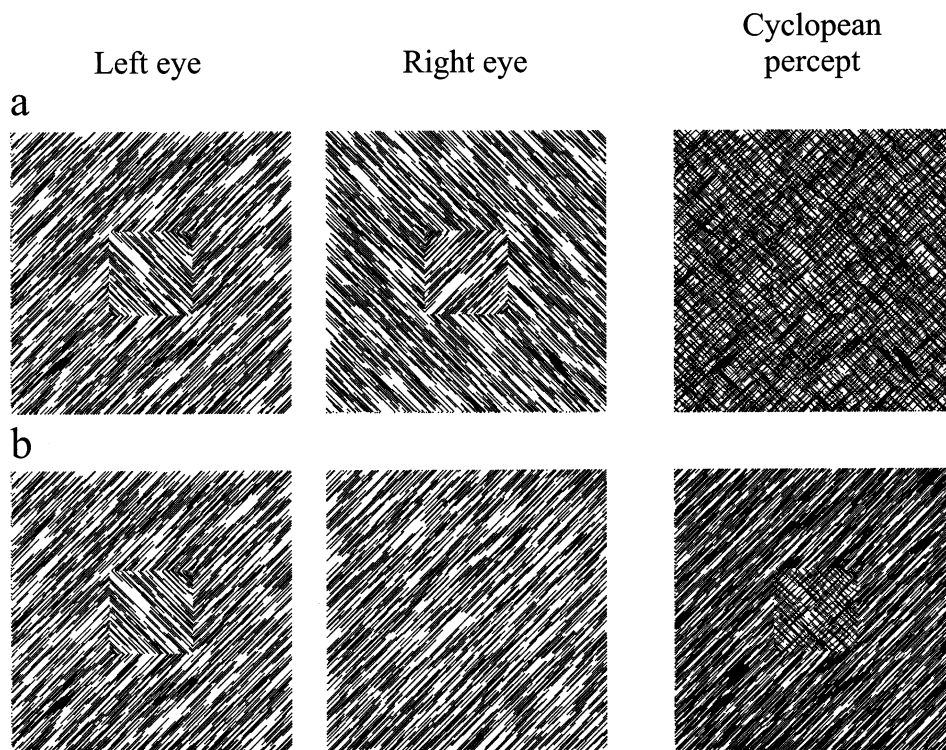


Fig. 4. (a) Orthogonal textures presented to the two eyes, each containing a figure on a background yield a cyclopean percept of a homogenous texture, with no visible figure (at excentric fixation). (b) When the figure is present in one eye only, the cyclopean percept is that of a figure on a background. The stimulus in (b) yields figure–ground related contextual modulation, the stimulus in (a) does not (Zipser et al., 1996).

al., this volume). Could it be that at some time, these neurons even express visual awareness? There are several converging pieces of evidence that indicate that this might very well be the case. First, there are stimulus manipulations that have strong effects on whether stimuli are perceived or not, and these seem to effect late onset modulations in particular. We did an experiment that was inspired by the stimuli used by Kolb and Braun to demonstrate blindsight in normal observers (Kolb & Braun, 1995). When two figure–ground displays with orthogonal orientations are presented each to one of the two eyes, the fused Cyclopean percept is that of a homogenous texture with no figure present in it (Fig. 4a). When one eye is presented with a homogenous texture and the other eye with a figure–ground display, the figure is visible (Fig. 4b). The latter stimulus evokes contextual modulation signalling the presence of the figure, but the former stimulus does not (Zipser et al., 1996); so while the figures are present in either eye alone the modulation signals the percept (no figure present) rather than this information. These findings may furthermore be associated with the results of Bridgeman (1980). He recorded from V1 neurons in awake monkeys while presenting stimuli that were masked using meta-contrast masking. The animals reported the masking behaviourally. The early responses of the V1 neurons (up to 110 ms) were not affected by the masking, but late responses (after 110 ms) were

inhibited by the masking, signalling the reduced visibility of the stimuli covering the receptive field (Bridgeman, 1980). A third example comes from the random dot patterns that evoke a depth percept when luminance correlated dot pairs are used, while no depth percept is evoked when anti-correlated dots are used. V1 neurons are equally well tuned to both of them, suggesting no role of the V1 depth responses in depth perception. However, when response amplitude is considered, it appears that the correlated dots produce about twice the response of the anti-correlated dots (Cumming & Parker, 1997). Depth perception rather than disparity as such thus has an influence on the V1 responses.

Of course the above examples are still manipulations of the stimuli rather than of visual awareness. A (rather crude) way of manipulating awareness is anaesthesia. While receptive field tuning properties of V1 neurons are little or not affected by anaesthesia (Schiller, Finlay & Volman, 1976; Snodderly & Gur, 1995), contextual modulation is affected by anaesthesia to different degrees. Short latency modulations, evoked by surround stimuli that may exert their effects through local or horizontal connections within V1, can be recorded in awake as well as anaesthetized animals (Knierim & Van Essen, 1992; Kapadia et al., 1995; Kastner et al., 1997; Polat et al., 1998). However, modulations reflecting perceptual pop-out are stronger in awake than in anaes-

thetized animals (Nothdurft et al., 1999). Finally, contextual modulation related to figure–ground segregation is fully suppressed by anaesthesia (Lamme, Supér & Spekreijse, 1998b). The latter type of modulation seems to depend strongly on feedback from extrastriate areas (Lamme, Zipser & Spekreijse, 1998c). It seems as if the longer information has to ‘travel’ over the network of local, horizontal, and feedback connections to evoke the modulatory effects, the more susceptible these effects are to anaesthesia.

Anaesthesia will not only affect visual awareness but probably many other processes as well. A more direct link to visual awareness would only be established when a trial by trial comparison of perceived versus not perceived stimuli, that are otherwise identical, is performed. This was recently done by using figure–ground displays like shown in Fig. 2. Contextual modulation was recorded in monkeys that had to report whether the figure was perceived or not. This was done in a manner very similar to the one used to demonstrate that monkeys do not ‘perceive’ stimuli in blindsight (Moore et al., 1995). Catch-trials, in which no figure was present at all, were presented in combination with figure-present trials, where a figure appeared at one of three possible locations. The animal’s task was to indicate the position of the figure, when present, by making a saccadic eye movement towards it. On catch-trials, the animal was rewarded when it remained fixating. The key feature of the paradigm is that when for some reason the figure in a figure-present trial is not perceived, the monkey will signal this by maintaining fixation. Neural responses recorded during figure-present trials that resulted in a correct saccade were compared with responses from figure-present trials that were classified as figure-absent (catch-trial) by the monkey. Figure–ground related contextual modulation was strongly reduced or absent in the case the monkey did not perceive the figure (Supér, Lamme & Spekreijse, 1999). In other words, contextual modulation only reflects the figure–ground relationships when these are (consciously) perceived by the animal.

Further evidence in the same direction comes from experiments that show that V1 responses are influenced by how ambiguous stimuli are perceived. As already mentioned, some 20% of V1/V2 cells are influenced by perceptual switches in binocular rivalry (Leopold & Logothetis, 1996). Likewise, it was shown that the responses of V1 neurons (Grunewald, Bradley & Andersen, 1999), just like MT neurons (Bradley, Chang & Andersen, 1998), are influenced by the perceived direction of rotation of a random dot cylinder whose rotation, clockwise or counter-clockwise, is perceptually ambiguous.

In summary, the responses of V1 cells indeed appear to be a mixture of activity that is not related to perception, and activity that correlates with aspects of

perceptual organization, attention, and visual awareness. Early response components are mostly related to receptive field based processing, far dissociated from perception, while late components of the V1 responses are correlated with conscious perceptual interpretations of the scene.

4. Conclusions

Here we will summarize several conclusions that have been drawn above on the basis of the neuropsychological, neurophysiological and other data.

1. *V1 is not an awareness dedicated area*

It is evident that V1 is not an awareness dedicated area in the sense that the activity of its neurons is necessary *and* sufficient to produce a conscious percept. This conclusion can be drawn from neuropsychological as well as from neurophysiological data; In other words, when V1 neurons fire we do not automatically become aware of the information that is conveyed by these neurons. So within the framework of the localizationist approach to the NCVA, the role for V1 seems rather limited.

In this respect, however, V1 seems hardly different from the other visual areas. The neuropsychological findings discussed above showed that in fact none of the visual areas, be it V1, the extrastriate areas, or any other high level area in the dorsal or ventral stream alone is sufficient to produce visual awareness.

2. *Synchrony in V1 is not a correlate of perceptual organization*

To date, there is still very little evidence that synchrony in V1 represents the final ‘outcome’ of the process of perceptual organization, let alone whether we are aware of this outcome. Many experiments show a relation between synchrony and rules of perceptual organization, but without dissociating it from a relation between synchrony and intrinsic V1 connections. Some results suggest that synchrony might go beyond intrinsic V1 connections and signal what is perceived (Fries et al., 1997), while other results suggest the very opposite, that synchrony in V1 reflect the intrinsic connections irrespective of how a scene is perceived (Lamme & Spekreijse, 1998a).

3. *V1 neurons express different aspects of visual processing at different times*

The activity of V1 cells represents local receptive field based processing at short latencies after stimulus onset, but at longer latencies represents various aspects of

perceptual organization, which we call contextual modulation. Finally, V1 activity may reflect whether stimuli are attended to or not. Also in this respect, V1 seems to be hardly different from other cortical areas. In parietal cortex, for example, it is found that neurons may represent aspects of the visual stimulus as well as activity related to saccadic eye movements targeted at these stimuli, and whether stimuli are attended to or not (Colby, Duhamel & Goldberg, 1996). This may not be considered very surprising for a cortical region that is clearly situated between sensory and executive space and that is known to play an important role in the transformation of information from retinal to motor coordinate frames (Andersen, Snyder, Li & Stricanne, 1993; Andersen, Snyder, Bradley & Xing, 1997; Colby, 1998). However, also at the other extreme end of the brain, in primary motor cortex, it is found that early responses in a sensorimotor task are reflecting the sensory events, while late responses are mostly reflecting the motor commands that conclude the task. At intermediate latencies, responses are reflecting intermediate stages of processing related to the specific sensorimotor mapping rules that apply to the task (Zhang, Riehle, Requin & Kornblum, 1997). In the frontal eye fields of prefrontal cortex, similar findings have been reported with respect to eye movements. Different types of neurons have been identified; visual neurons, and pre-saccade neurons (Schall & Thompson, 1999). Visual neurons may reflect different stages of the visuo-motor transformation at different moments in time. In a task where monkeys had to select the odd item amongst a set of distractors, the visual response up to 120 ms did not differentiate between target and distractors. After 120–150 ms, however, the visual neurons had a much larger response to targets than to distractors (Thompson, Hanes, Bichot & Schall, 1996; Schall & Bichot, 1998).

That neurons at one moment may be engaged in sensory processing while at another moment may be involved in the neural processes generating a behavioural response has an important consequence for the search for the NCVA; when some part of the activity of an area or even a cell has been proven not to correlate with awareness this never logically warrants the conclusion that the cell is not part of the NCVA. It might very well be, just at some other moment in time. To exclude a neuron from the NCVA it would have to be shown that it is not at any time correlated with awareness, in any kind of visual task. This is obviously an impossible enterprise.

4. *Some part of V1 activity reflects visual awareness*

We have seen that a percentage of V1 cells may reflect the reported percept in rivalry experiments or in experiments using ambiguous motion stimuli. Also,

contextual modulation for figure–ground displays only occurs when the animal reports to be aware of the figure. There are some noteworthy similarities in this respect with neural correlates of visual awareness that have been recorded in prefrontal cortex. Neural activation in the frontal eye field was studied in relation to the detection of masked stimuli (Thompson & Schall, 1998, 1999; this volume). It was shown that visual neurons in the early parts of their response exhibit activity that ‘predicts’ whether the monkey will detect the target. Moreover, components of the response after about 100 ms correlate with whether the monkey identifies the stimulus as a target or not. There are several reasons to argue that this late activity is not a correlate of the eye movement associated with the target identification but rather is a correlate of the conscious visual selection process leading to the distinction between targets and non-targets (Thompson and Schall, this volume).

Prefrontal cortex projects back to extrastriate visual areas (Salin & Bullier, 1995), and there is evidence that contextual modulation in V1 depends on feedback (Bullier, Hupé, James & Girard, 1996; Lamme et al., 1998c; Hupé, James, Payne, Lomber, Girard & Bullier, 1998). This suggests that the late onset modulations observed in prefrontal cortex and in V1, which both relate to whether stimuli are perceived or not, strongly interdepend. Obviously the many visual and sensorimotor areas in between these two extreme ‘ends’ of the brain will be involved as well, as is shown by the many findings of correlates of subjective perception in the extrastriate areas (Logothetis & Schall, 1989; Leopold & Logothetis, 1996; Britten, Newsome, Shadlen, Celebrini & Movshon, 1996; Bradley et al., 1998). Many theories of visual awareness propose a general ‘state’ of activity that involves many areas of the brain simultaneously, and that is achieved by recurrent feedforward–feedback connections, the key feature of this state being some sort of resonance (Pollen, 1999), or reentry (Edelman, 1992). The combination of related findings on V1 and frontal cortex provides evidence for such models.

The fact that in V1, as well as in many other corticale areas a *percentage* of the activity correlates with awareness poses a difficult problem for the localizationist approach to visual awareness. It is probably safe to say that in all parts of the brain activity may be recorded about events of which we are not aware. Similarly, maybe in all areas of the brain, activity can be recorded that *is* related to awareness. This makes it rather difficult to draw a sharp line to demarcate areas that belong to the neural substrate of visual awareness from those that do not. One would have to set a rather arbitrary threshold on the percentage of activity that should be related to conscious events in order to include the area. Moreover, any such a threshold will

probably include and exclude different areas, depending on the stimulus or task that is used.

5. The role of V1 in the NCVA depends on how the NCVA is mediated

When acknowledging the first four conclusions, it is evident that the answer to the question whether V1 plays a role in visual awareness cannot be answered before we know *how* visual awareness is mediated. When awareness turns out to be mediated by some specific cortical area or some specific set of cells, V1 will not be part of such a correlate of awareness. Also when the NCVA turns out to be synchrony (or synchronous oscillations in some specific frequency range), V1 will probably not be part of it. However, when the NCVA will consist of modulations of firing rate, very much like the neural correlate of visual attention, V1 will probably play as much a role as any other area of the brain. The question *how* the NCVA is mediated should thus logically precede the question *where* it is localized. As long as we are as far removed from an answer to this 'how' question as we are today, excluding V1 from the NCVA is premature and may in fact obscure the way towards that answer.

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